THE REACTION-TIME OF GONIONEMUS MURBACHII TO ELECTRIC AND PHOTIC STIMULI.[1]

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CONTENTS.

Problems and Methods.

The reaction-time method as applied to the study of the functioning of the nervous system has already given us certain important facts in human neuro-physiology, and it promises much more valuable results when its application to representatives of the various animal phyla makes a comparative survey of the time relations of neural processes possible. The value of reaction-time studies lies chiefly in the knowledge which they give us of the biological significance of the nervous system. "Certainly they are not important as giving us knowledge of the time of perception, cognition or association, except in so far as we discover the relations of these processes, and the conditions which are most favorable for them. To determine how this or that factor in the environment influences the activities of the nervous system, and in what way system may be adjusted to system or part process to whole is the task of the reaction-time investigator."[2]

For the reaction-time measurements which furnish the material of this paper chronoscopic methods were employed. All reactions to light were measured by means of a stop watch readable to tenths of a second, but for the reactions to electric stimuli, which were very much quicker, it was necessary to make use of

[1] From the Marine Biological Laboratory, Woods Holl, Mass.

[2] Yerkes, Robert Mearns: "The Instincts, Habits and Reactions of the Frog." *Harvard Psychological Studies*, Vol. I., 1903, p. 509 (*Psychological Review Monograph Supplement*, Vol. IV.).

an instrument readable to hundredths or thousandths of a second. For this purpose a Hipp chronoscope, readable to thousandths, was placed in circuit with the stimulus electrodes and the reaction-key. The electrodes were connected in such a way that the chronoscope circuit was made, and the record thereby started, the instant the stimulus circuit was completed. The motor reaction of the medusa in response to the electric shock served to break the chronoscope circuit, thus stopping the record. The experimenter was then able to read from the chronoscope dials the time which intervened between stimulus and reaction (reaction-time). Cattell's falling screen served as a regulator for the chronoscope.[1]

The reaction-key used in these measurements of the time of reaction to electric stimuli consisted of a frame for the support of an easily sliding rod, one end of which carried a cork disk and the other a platinum point by which the circuit was completed. The movement of the medusa against the disk when a stimulus was given, caused the rod to slip upward, thus breaking the chronoscope circuit.

Reaction-Time to Electric Stimuli.

Gonionemus reacts to an electric current, indirectly applied, in from one to five seconds, according to the strength of the stimulus, and the position of the electrodes. The following averages indicate the facts. Since it was not possible to get more than four or five satisfactory reactions in series with any one animal, the averages, unless otherwise marked, are for five reactions.

I. Reactions to a 4-Mesco-cell current, with electrodes on opposite sides of the bell, not in contact with the organism. M. 1.023 sec.; M.V. 0.168 sec.; R.V.[2] 16.0.

II. Same, with 2-cell current. M. 1.489 sec.; M. V. 0.199 sec.; R. V. 13.4.

III. Reactions to a 4-cell current, with electrodes 5 mm. apart in contact with the margin of the bell. M. 0.605 sec.; M. V. 0.128 sec.; R. V. 21.

Repetition of the 4-cell stimulus at intervals of a minute causes

[1] For fuller description of the chronoscopic method used see *Harvard Psychological Studies*, Vol. I., pp. 601–605.

[2] R.V. = (M.V. $\times$ 100) / M. = Relative Variability.

a rapid lengthening of the time of reaction. Thus: first reaction, .506 sec.; second, 1.003; third, 3.607.

As compared with the reactions of the small medusa *Gonionemus*, those of the jelly-fish *Cyanea arctica* are slow. Some individual reaction-times of a single individual (*Cyanea*) to a four-cell current, with electrodes in contact with opposite points on the margin follow.

Reaction.	Reaction-Time.	Deviation from Mean.
1	1.026 sec.	.504 sec.
2	1.987	.457
3	1.324	.206
4	1.636	.106
5	1.629	.099
6	1.760	.230
7	1.200	.330
8	1.328	.202
9	1.800	.270
10	1.610	.080
Mean.	1.530	Mean variation. .248

Relative Variability 16.2.

Reaction-Time to Photic Stimuli.

The reaction-time of *Gonionemus* to increase in light intensity, as I have stated in another paper,[1] varies with the strength of the stimulus, temperature, condition of the organism, etc., from one to thirty seconds. To daylight the organism usually responds in about seven seconds; to sunlight the reaction is at first much quicker, but it rapidly lengthens as the organism is exposed to the influence of the intense light. The relation of time of reaction to intensity is indicated by the following averages: Weak daylight, 9.4 sec.; daylight, 7.0 sec.; sunlight, 5.5 sec.

Moreover, the reaction-time varies with the size, sex, and pigmentation of the individual, as well as with such external conditions as temperature, density, and chemical constitution of the medium. Increase in temperature gradually shortens the time from about 8–9 sec. at 19° C., to 2–3 sec. at 32° C. Decrease in temperature lengthens the time, until reactions fail entirely at about 10–12° C.

[1] Yerkes, Robert M., with the assistance of James B. Ayer, Jr.: "A Study of the Reactions and Reaction-Time of the Medusa *Gonionema murbachii* to Photic stimuli." *Amer. Journ. Physiol.*, Vol. 9, 1903, pp. 279–307.

Between these reaction-times of the Cœlenterata and those of most vertebrates, as well as of many invertebrates, there is a striking difference in rapidity. Whereas, the jelly-fish and medusa respond to an electric stimulus in from one to four seconds, the fish or frog responds in a fraction of a second, usually not more than one fourth, and sometimes one tenth. Observe the reaction of the fiddler crab to a shadow, and note how quick it is in comparison with the reaction of *Gonionemus* to the same change in illumination. Is this difference in reaction-time due to a difference in sensitiveness (*i. e.*, is the latency period of stimulation longer); is there a difference in the rate of impulse transmission, of central nerve processes, or of muscle contraction? Such questions should be answered by means of reaction-time investigations. The rate of impulse transmission (presumably nerve transmission) is much slower in the medusa *Gonionemus* than in the vertebrates and most invertebrates thus far studied. Furthermore, it differs for different regions of the medusa; the margin and the radial

Frog.				Medusa.			
Electric Stim. Intensity.	M.	M. V.	R. V.	Light Intensity.	M.	M. V.	R. V.
1	.301 sec.	.085 sec.	28.2	Weak daylight.	9.4 sec.	3.16 sec.	33.6
2	.231 "	.034 "	14.7	Daylight.	7.0 "	2.39 "	34.1
4	.103 "	.012 "	11.6	Sunlight.	5.5 "	1.60 "	29.0

canal regions transmit impulses much more rapidly than do the inter-radial regions. The exumbrellar layer of tissue, so far as I have been able to determine, does not transmit impulses at all.[1]

The frog reacts to such an electric stimulus as was applied to *Gonionemus* in .150–.200 sec. In comparison the medusa's reaction-time is very long; but it differs in yet another respect—it is far more variable. The reaction-times and variabilities of the reactions of frogs to three intensities of electric stimulation as determined in an experimental investigation[2] are here given for comparison with the results given by *Gonionemus* to three intensities of light.

[1] Yerkes, Robert M.: "A Contribution to the Physiology of the Nervous System of the Medusa Gonionema Murbachii. Part II.—The Physiology of the Central Nervous System," *Amer. Jour. Physiol.*, Vol. 7, 1902, p. 193.

[2] *Harvard Psychological Studies*, Vol. I., 1903, pp. 616–618.

This table shows that the relative as well as the absolute variability is higher for the medusa than for the frog. In general it is true that variability increases with increase in the time of reaction. Stimuli or intensities of stimulation which give extremely short reaction-times may be expected to give low indices of variability; similarly animals which are slow in reacting exhibit high degrees of variability. The reflex reaction is absolutely and relatively the least variable among the common types of action; the instinctive reaction is much more variable, and most variable of all in time of execution as also in form, is the voluntary reaction so-called

Relation of Reaction-Time to Region Stimulated.

As might be expected the reaction-time of *Gonionemus* varies with the region stimulated. When the electrodes are placed in contact with the margin at the bases of the radial canals the reaction is noticeably quicker than when the inter-radial regions or other portions of the bell are stimulated. The average reaction-time to a four-cell current applied to the inter-radial portions of the margin is .605 second; for the radial canal regions it is .507 second. It is not necessary, however, to make measurements to thousandths or even hundredths of a second to exhibit this fact; stimulating different regions and simply watching the responses will make clear the differences in reaction-time. Again the time of reaction to light varies according as the light falls upon the subumbrellar or the exumbrellar surfaces. It is much shorter when the subumbrella is exposed to the light (3.4 seconds as compared with 17.4 seconds for the other position).[1]

It is not at all likely that the differences in reaction-time here noted for electric and photic stimuli are due to the same conditions. The quicker reaction to stimulation of the radial canal regions is doubtless due to the higher transmission rate of the differentiated nerve tracts along the radial canals. Stimulation of any other portion of the bell causes reaction less quickly simply because the tissues transmit impulses less rapidly, since they possess less highly specialized nerve tracts. In case of the quicker reaction to light when the medusa is resting with the

[1] *Amer. Jour. Physiol.*, Vol. 9, 1903, p. 301.

subumbrellar, instead of the exumbrellar, surface toward the light, a difference in sensitiveness is apparently the cause of the difference in reaction-time. Certain organs which are especially sensitive to light are found on the subumbrellar surface of the margin, and it is when they are most fully exposed to the action of light that the organism responds most promptly to the stimulus. The rate of impulse transmission is probably the same no matter which surface is stimulated by light, but the latency period of stimulation is far greater for stimulation of the exumbrella.

These experimentally demonstrable facts clearly prove that the nervous system of the medusa *Gonionemus* consists of cells which possess irritability and conductivity in high degrees. And they further show that rapidity of reaction is directly dependent upon specially differentiated paths of conduction.

Reaction-Time of Tentacles.

A study of the reaction-time of the various parts of *Gonionemus* (tentacles, manubrium, margin, bell), when normally functioning, and when isolated by operation, throws interesting light upon certain problems in the physiology of the nervous system.

Cutting off the tentacles close to the bell causes *Gonionemus* a severe shock. If only one tentacle is cut off the usual response is a contraction of the bell, which may occasionally lead to a swimming bout. The severity of the shock, or as we would commonly say, the strength of the stimulus which *Gonionemus* receives from tentacle excision, evidently varies directly with the size of the organ. Small tentacles frequently may be cut without causing any visible reaction except slight contractions of the adjacent tentacles; large tentacles cause one or more contractions, and in general the larger the organ the greater the number and force of the contractions. Excision of the primary tentacles, those at the bases of the radial canals, apparently causes the most severe shock, for when one of them is suddenly clipped off the animal frequently swims about rapidly for a considerable length of time. In every way its reaction is more vigorous than those caused by excision of smaller tentacles or of large tentacles in other positions.

It would appear from this that the radial canal tentacle is of

special significance in the life of the medusa. And in support of this belief it is worth noting that they are almost always held differently from the others. When the majority of the tentacles of a "bell up" (exumbrellar surface uppermost) individual are resting on the bottom of the vessel, the primary tentacles are usually held slightly higher in the water than the others. They are used for attachment and for food seizing sooner than the others. These facts point toward either a specialization or a modification in function which is of interest because of its bearing upon certain neuro-anatomical facts which have been presented by Miss Hyde.[1] She finds well-defined cell-fiber tracts along the radial canals. This being the case we should expect the radial canal tentacles to have a more important and direct influence upon the reactions of the organism than have the other tentacles.

When the medusa is stimulated to motion by light the tentacles contract from .1–.2 second before the bell. At times tentacle reactions occur in the absence of a general bell contraction. As determined with a stop-watch the reaction-time of the normal

I. Reaction-Time of Normal Tentacles to Daylight.

Tentacle.	M.	M. V.	R. V.
No. 1	2.2 sec.	0.22 sec.	10.0
" 2	3.4 "	0.62 "	18.2
" 3	3.6 "	0.46 "	12.6
General averages.	3.1 —	0.43 +	13.6

II. Reaction-Time of Tentacles of Excised Margin to Daylight.

Tentacle.	M.	M. V.	R. V.
No. 1	2.5 sec.	0.16 sec.	6.4
" 2	2.7 "	1.06 "	39.2
" 3	2.9 "	0.79 "	27.2
General averages.	2.4 —	0.67 "	24.3

II. Reaction-Time of Excised Tentacles to Daylight. (Average of First Three Reactions.)

Tentacle.	M.	M. V.	R. V.
No. 1	5.3 sec.	2.30 sec.	43.4
" 2	4.2 "	1.92 "	45.2
" 3	4.4 "	1.33 "	30.2
General averages.	4.5 —	1.85 "	39.6

[1] Hyde, Ida H.: "The Nervous System of Gonionema Murbachii," Biological Bulletin, Vol. IV., 1902, pp. 40–45.

tentacle to the increase in light intensity caused by suddenly uncovering a dish containing the medusa is from two to five seconds. Reaction-time averages for three conditions of the tentacle are given in table on page 90.

A fact significant in this connection is that the excised tentacle rapidly loses its power to react to photic stimuli. To the first four or five repetitions of a stimulus it usually reacts quickly, then the time of reaction, as is shown in the series herewith presented, rapidly increases until reaction fails entirely.

SERIES OF REACTIONS OF AN EXCISED TENTACLE TO DAYLIGHT.

Reaction	1	4.6
"	2	2.5
"	3	8.7
"	4	15.6
"	5	35.0
"	6	No reaction except to
"	7	mechanical stimulation.

The reaction-time of the normal tentacle, 3.1 seconds, is considerably shorter, as would be expected, than that of the bell. Its variability is low. The reactions of the tentacles of excised margins are slightly quicker, 2.4, according to the results presented, than are those of the normal animal, but they are also more variable. The quickness of these reactions may possibly be due to a temporary increase in the irritability of the margin caused by the operation. Finally, the reactions of excised tentacles are much longer, 4.5, and more variable than are those of either the normal animal or the excised margin. This may mean that the tentacle contraction in response to light is normally initiated by stimulation of the margin, or that the ability of the organ to react is lessened by its separation from the bell. At any rate there is a marked difference here indicated in the time of reaction of isolated and normally attached organs, a difference which may possibly be an indication of a function of the central nervous system or of the special organs of light stimulation which are in all probability situated in the margin of the bell.

RELATION OF QUALITY OF STIMULUS TO TIME OF REACTION.

The motor reaction of *Gonionemus* to increase in light is much slower than that to other forms of stimuli. This is due in part

to difference in strength of stimulus, but it is of interest to enquire whether the quality of the stimulus is not of importance. We may ask, for example, whether the reaction-time to the threshold stimulus of all modes of stimulation is the same. If it is not, quality of stimulus is evidently significant. Wundt[1] presents the following figures in support of his statement that the reaction-time to the threshold intensity of all modes of stimulation is the same.

Threshold Stimulus.	Mean.	Mean Variation.
Sound.	.337 sec.	0.50 sec.
Light.	.331	0.57
Touch.	.327	0.32

The results which I have gotten with frogs in working with electric and tactual stimuli cause me to question the applicability of this statement to the reactions of all organisms. It seems highly probable that the just perceptible stimulus reaction-time is by no means the same for different qualities of stimulus. Those modifications of the vital processes which make survival possible appear even in the responses to minimal stimuli. In one case the just perceptible stimulus may cause nothing more than a slight local change in circulation, excretion, muscular action, in another it may produce, just because of the particular significance of the stimulus for the life of the organism, a violent and sudden motor reaction.[2]

Absolute and Relation Variability.

As already pointed out[3] it is generally useless to compare reaction-times with respect to variability unless the reaction-time value as well as the absolute variability is considered. If, for example, to an electric stimulus *Gonionemus* reacts in 2.0 seconds, with a variability of 0.5 sec.; and to a photic stimulus in 6.0 seconds, with a variability of 1.5 sec., it is not correct to say that the reaction-time to light is three times as variable as that to electricity. As a matter of fact the two variabilities as such are

[1] Wundt, Wm.: "Grundzüge der physiologischen Psychologie," Fünfte Auflage, Leipzig, 1903, Dritte Band, S. 428–429.

[2] *Harvard Psychological Studies*, Vol. I., 1903, p. 625.

[3] *Amer. Jour. Physiol.*, Vol. 9, 1903, p. 291.

not equal, but when we consider the reaction-times we find that the ratio of variability to reaction-time is in each case 1 : 4. Although the absolute variability is in one case three times as great as in the other, it is 25 per cent. of the average reaction-time in both instances.

Heretofore I have expressed relative variability as a ratio (M.V. : M.), or as a percentage value of the mean (M.V. = x per cent. of M., in which case x = R.V., the relative variability.)

Obviously it is always important in comparative reaction-time work to know the relative variability of reactions ; in fact it is often quite impossible to make significant comparisons of results until this value is found. For this reason I have given in every table of this paper the percentage value of the mean variation in terms of the mean. This value I have called the relative variability (R. V.). It is obtainable by the formula recently used by Myers,[1] v.c. = m.v. × 100 / av. In this formula, which as inspection shows gives the ratio (in per cent.) of m.v. to av., v.c. is a value called by Myers the variation-coefficient, and av. is the mean (M.). Supposing a reaction-time of .180 second to have an absolute variability of .020 second, then by the formula (.020 × 100 / .180) the variation-coefficient (Myers), or what I prefer to call the relative variability (R. V.), is 11.1 + . If we chose this value might be written 11.1 + per cent., thus indicating that the absolute variability (M. V.) is 11.1 + per cent. of the average reaction-time (M.).

Since Pearson[2] in this statistical work has made use of a quantity which he calls the "coefficient of variability," and which is obtained by the formula

$$\text{C. V.} = \frac{\dfrac{\sqrt{\Sigma(x^2 \cdot f)}}{n}}{\text{M.}} \times 100,$$

it seems unwise to use the term variation-coefficient, suggested by Myers, for this new quantity in reaction-time work. As the value which we obtain by Myers' formula is in reality the per-

[1] Myers, Chas. S.: "Reports of the Cambridge Anthropological Expedition to Torres Straits." Vol. II., "Physiology and Psychology," Part II., 1903, p. 212.

[2] Pearson, Karl: "Mathematical Contributions to the Theory of Evolution, III., Regression, Heredity and Panmixia," *Phil. Trans. Roy. Soc. London*, Vol. 187, A, pp. 253–318.

centage value of the mean variation in terms of the mean, I see no reason why we should not call it the relative variability, in contrast with the absolute variability. Thus the confusion with Pearson's quantity which will inevitably result from the use of variation-coefficient can be avoided.

Myers' formula gives us precisely what we need for the direct comparison of reaction-times, with respect to their variableness, either to different stimuli or of different organisms. Strange to say most investigators of the time relations of neural processes have paid little or no attention to the variability of their results; none, so far as I know, have ever determined the relative variability throughout their work. It may be objected that those who have use for the relative variability can find it for themselves since the reaction-time and its mean variation are usually given. But the value is far too important to be left half-way determined; in fact it is even more useful in most cases than the mean variation. Every one who has had experience in dealing with reaction-time results will admit that the reaction-time to a particular stimulus has different meanings according to its variability, and that it is never possible to compare reaction-times without considering this value. It is clear then that *no reaction-time statistics should be published without determinations of the relative variabilities.*

Conventionally we compare human reaction-times to visual, tactual and auditory stimuli without noticing their variabilities or the strength of the stimulus employed. Jastrow[1] in a table of results, collected from the papers of many investigators, which is intended to indicate the differences in time of reaction for the different senses gives these averages: Visual reaction-time .185 second; tactile, .148; auditory, .139. Not even the mean variability is given in connection with the averages. Since reaction-time varies with the strength of the stimulus it is possible by varying the stimulus-intensity to get any one of the above reaction-times with any of the qualities of stimulus named. This being true, how are we to make valuable comparisons of reaction-times to different kinds of stimuli?

As before stated the threshold intensities of all modes of stimulation may be regarded as directly comparable. No matter what

[1] Jastrow, Joseph: "The Time Relations of Mental Phenomena," New York, 1890, p. 11.

the form of the stimulus, the threshold gives the longest and most variable reaction-time which can be obtained by the use of that particular quality of stimulus. Now, as the intensity of the stimulus is increased the variability decreases. Why may we not choose equality in relative or in absolute variability as a basis of comparison? If it should be found—and I am now gathering data for the settlement of the point—that the relative variability is the same for the threshold reaction-time to all qualities of stimuli, equality in relative variability would be the most satisfactory basis; if, on the other hand, absolute variability is a constant quantity at the threshold, it should be used in preference.

NOTE.—Reasons have recently appeared for returning to the original spelling of the name of the medusa. *Gonionemus* therefore is used instead of *Gonionema*.